HIGH MORTALITY OF PIPING PLOVERS ON BEACHES WITH ABUNDANT GHOST CRABS: CORRELATION, NOT CAUSATION

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ABSTRACT.—Ghost crabs (*Ocypode quadrata*) have been implicated in mortality of eggs and chicks of the beach-nesting Piping Plover (*Charadrius melodus*) whose Atlantic Coast populations are listed as threatened. Through observation and experimentation, we investigated the interactions between ghost crabs and plovers on Wild Beach, a Piping Plover nesting area on Assateague Island, Virginia. This site has a high abundance of ghost crabs and historically low fledging success compared to adjacent areas with fewer crabs. We observed encounters of crabs with plover eggs, chicks, and adults in the field, but never predation. In staged encounters of crabs with eggs and chicks (using hatchery reared quail as plover surrogates), we were unable to elicit predatory behavior either on the beach or in the lab. We conclude that although instances of ghost crab predation on Piping Plover eggs and chicks occur, they are rare and cannot account for the high mortality frequently reported on beaches where ghost crabs are abundant. Adult plovers behave toward crabs as if they were dangerous to eggs and chicks, and their young broods in the study area did not forage along the foreshore. Hence, ghost crabs may increase mortality indirectly. Frequent responding to crabs by parents may attract more deadly brood predators. Brood nutrition may suffer as adult plovers direct chicks away from areas where forage is reportedly richer but crabs are abundant, such as the foreshore. Nutrient intake may be further reduced on more southerly breeding grounds where high temperatures on backshores force chicks to stop foraging and take shelter during mid-day. Although high mortality cannot be attributed directly to predation by crabs, it may be due to factors that covary with crab abundance, such as high temperature, behavioral responses of adult birds, and poor forage. *Received 28 April 1998, accepted 7 Feb. 1999.*

Anecdotal and published reports of ghost crab predation on Piping Plovers (*Charadrius melodus*; Loegering et al. 1995, Watts and Bradshaw 1995) have led to concern that crab predation may hamper recovery of plovers on the Atlantic Coast, where the species is listed as threatened (Loegering and Fraser 1995; U.S. Fish and Wildlife Service 1993, 1996). To assess the extent of crab-caused mortality, we investigated interactions between ghost crabs (*Ocypode quadrata*) and Piping Plovers during incubation and chick rearing on Wild Beach on Assateague Island, Virginia, within the Chincoteague National Wildlife Refuge. Compared to other portions of this barrier island that are used for nesting areas by the Piping Plover, Wild Beach has higher abundances of ghost crabs (Britton 1979) and lower rates of fledging success (U.S. Fish and Wildlife Service 1994).

Piping Plovers breed from eastern Canada to North Carolina, as well as in the Great Lakes region and the Great Plains of Canada and the U.S. (Haig 1992). On the Atlantic Coast, plovers typically lay four eggs in a shallow scrape in the sand, usually well beyond the high-tide mark, or in shelly storm-flattened areas (washouts) between and behind the primary dunes. Chicks are precocial and forage in moist backshore areas where available, or on the foreshore (the area between the tides; Loegering and Fraser 1995).

Ghost crabs, named for their cryptic coloration, range along the Atlantic Coast from Rhode Island to Brazil and throughout the Caribbean (Chace and Hobbs 1969). They are among the fastest terrestrial invertebrates (Full and Weinstein 1992) and formidable predators with acute sensory receptors for vision, vibration, taste, and smell (Cowles 1908, Wellins et al. 1989). They are most abundant on high energy beaches, where they obtain over 90% of their diet preying on intertidal invertebrates (Wolcott 1978). They are extremely flexible foragers, also scavenging, deposit feeding, consuming seeds and insects, and are documented predators of turtle hatchlings (Arndt 1994, Robertson and Pfeiffer 1982). At dusk crabs move from their burrows on the backshore and among the dunes to feed in the swash zone. Crabs seek out and take refuge in burrows as dawn approaches (Wolcott 1978).

Poor fledging success on beaches where crabs are abundant, coupled with extensive

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seasonal and spatial overlap between plovers and the predatory ghost crabs, led to the hypothesis that ghost crab predation is a common source of mortality for plover eggs and chicks (U.S. Fish and Wildlife 1993, Loegering and Fraser 1995). To test this hypothesis, we documented and quantified natural encounters between crabs and Piping Plover eggs and chicks, and staged encounters between crabs and the eggs and chicks of non-threatened species.

METHODS

We conducted our study on a 6.4 km stretch of the Chincoteague National Wildlife Refuge's (NWR) Wild Beach, Virginia, in June and July, 1994. Wild Beach has a steeply-sloped foreshore rising from a high energy surf zone to the berm and was characterized in 1994 by one or two wave-cut scarps less than 1 m high. At the berm the slope decreased abruptly and there was a narrow (20–50 m), flat backshore region. Inland of the backshore are low vegetated foredunes, fronting 2–4 m high artificially stabilized dunes vegetated with beach grass (*Ammophila breviligulata*) and seaside goldenrod (*Solidago sempervirens*).

We observed four natural plover nests through the last days of incubation and past hatching using continuous video monitoring to document crab predation on eggs and newly hatched chicks. When the third egg was laid in each nest, staff from the refuge surrounded the nest with a 4 m diameter, 1.5 m high exclosure constructed of 5 × 10 cm welded mesh wire supported by reinforcing bar and covered with plastic netting. A dummy camera was mounted at the top of an exclosure support bar on the southwest side, facing toward the nest and away from the prevailing wind. At the time nest observation began, the dummy camera was replaced with a similar appearing video surveillance camera fitted with infrared light-emitting diodes for nocturnal illumination, and an infrared filter to prevent saturation in strong sunlight. The camera imaged an area approximately 2 × 3 m centered on the nest. Installing the camera in place of the dummy took 3–12 min, and birds returned to the exclosure 1–9 min thereafter (mean = 4.25 min., *n* = 4). Coaxial and power cables (150 m) led to a TV/VCR (Magnavox model CCR095) powered by a deep-cycle lead-acid battery. These were housed in a tent behind nearby dunes to reduce disturbance to the plovers. Tapes were changed at six-hour intervals and the battery every 18 hours. According to the video record, the incubating adult plovers typically did not flush from the nest at those times. Video tapes were reviewed for the following occurrences and the times logged: adult plover brooding, alarming and flushing from the nest (rapid rising off eggs, standing near nest with wing raises, rapid exit from the field of view), parental exchanges of incubating/brooding duty (second parent appears on screen and changes places with the bird on the nest), eggs

hatching, activities of chicks (including walking, foraging and being brooded), and any activities of ghost crabs.

To explore the role of crab predation after chicks left the nest, we observed encounters between crabs and adult plovers and chicks for eight days, concentrating on periods of peak crab activity. Observations of hatched broods were made from a vehicle at least 30 m away, using binoculars during daylight hours, and an image-intensifying scope (Varo Noctron IV) at night fitted with an infrared diode laser to enhance illumination. Plover chicks in two broods were marked on each thigh with 10 mm diameter disks of Scotch-lite® (3M) reflectorized tape glued to the surface of their down to make them visible with night vision equipment. Two of the marked chicks were the only chicks to fledge in the study area; thus the treatment did not appear to increase mortality. Data collected during each observation period included the location of the brood, the place and time spent foraging, and the location of brooding.

To further assess the probability of ghost crabs preying on eggs, we presented crabs with surrogate eggs that were similar in size and shape to those of *Charadrius melodus* (see MacIvor et. al. 1990). Japanese Quail (*Coturnix japonicus*) eggs were obtained from a local bird breeder, and Northern Bobwhite (*Colinus virginianus*) eggs were obtained from Seven Oaks Game Farm and Supply, Wilmington, North Carolina. On three nights, we constructed four scrapes near the berm and placed four *Coturnix* eggs in each just prior to the time that crabs emerge from their burrows. During the nocturnal peak in crab activity (19:30–22:00 EST), the artificial nests were observed for any ghost crab encounters using the video camera unit fixed on a tripod.

To further explore the vulnerability of eggs to ghost crab predation, we placed four opaque gray plastic bins (38L × 18W × 11D cm) in a rectangular array in the laboratory and filled them to a depth of about 3 cm with damp sand from the foreshore. In each we placed a ghost crab [average weight 49.0 ± 5.4 (SD) g, with a carapace width of 43.2 ± 1.6 mm, *n* = 8] freshly-collected from the foreshore of Wild Beach, two *Coturnix* eggs, and the bins were covered with chicken wire. Crab activity was recorded using the infrared camera and VCR from the initiation of the experiment at 23:15 until 05:15, and condition of the eggs was assessed at 10:00. The experiment was repeated using dry beach sand and *Colinus* eggs on another night, and condition of the eggs assessed after 11 hours of exposure to the crabs. From the video tapes we noted the length of time crabs spent in contact with eggs, their behavior, and the condition of the eggs after manipulation by the crabs.

To elucidate potential predatory interactions between crabs and chicks, we used chicks of Northern Bobwhite as surrogates for Piping Plover chicks. Bobwhite chicks are similar in size and behavior to Piping Plover chicks, but darker and hence less cryptic on beach sand. Two- and three-day-old chicks (*n* = 14)

were released near the beach berm into areas of high crab activity to maximize encounters with crabs and were observed with binoculars as they wandered on the beach. In four cases, chicks were deployed from the parked vehicle (to which crabs showed little response) into the immediate vicinity of active crabs. To verify that crabs were motivated to forage, we placed dead chicks, freshly cracked oysters, and pieces of thawed chicken upwind near the mouths of occupied burrows at the same time that live chicks were released onto the beach. Encounters between crabs and chicks and dead prey were documented.

To determine temporal overlap in activity between crabs and plovers, nocturnal and diurnal observations of crab activity and behavior were conducted from a vehicle. The onset of migration of crabs to the surf zone for nocturnal foraging was determined by noting the time of appearance of the first crab moving down the beach each night.

Statistics are reported as mean plus or minus one standard deviation.

RESULTS

Predation by crabs on eggs.—Ghost crabs did not prey on eggs in either natural nests or in experimental trials, and crabs showed comparable behavior toward eggs in all settings. In 147 hours of video observations of incubation by Piping Plovers, there were seven appearances of ghost crabs in the video field. These appearances generally were confined to the periods of crepuscular movement by the crabs (dawn, 04:16 ± 11.3 min, $n = 2$ and dusk, 20:01 ± 4.6 min, $n = 3$). Two exceptions occurred on one rainy day when high humidity and reduced insolation resulted in diurnal crab activity. In two cases, crabs directly contacted and manipulated the eggs in the nest cup after the incubating adult had flushed from the nest. Crabs appeared to be testing the eggs as potential prey, using chelae and mouthparts which contain dense arrays of chemoreceptors to "taste" the eggs. The durations of manipulations were 13 s and 23 s.

Crabs that contacted *Coturnix* eggs in pseudo-nests in the field either continued slowly toward the foreshore or stopped to manipulate and taste the eggs. Crabs spent more time in contact with eggs when manipulating them (17.3 ± 3.06 s, $n = 3$) than when they were not manipulating them (11.4 ± 8.4 s, $n = 5$). In one instance, a crab spent 6 minutes and 12 seconds at a pseudo-nest of *Coturnix* eggs on the beach, repeatedly tasting the eggs and rolling one egg several cm prior to moving on to the surf zone. We interpret this intense in-terest as a response to the bird feces present on that particular egg.

Crabs confined with *Colinus* eggs in the laboratory explored the eggs as potential prey at least once, not necessarily on the first contact, but simply walked over the eggs in other encounters. Four crabs spent an average of 12.2 s (± 8.2 s, $n = 11$), 10.6 s (± 11.2 s, $n = 8$), 6.9 s (± 6.7 s, $n = 10$), and 7.3 s (± 5.9 s, $n = 6$) on eggs per encounter. Average time of encounters in which manipulation occurred (all crabs) was 13.7 s (± 8.4 s, $n = 7$).

Potential for predation by crabs on chicks.—Three different Piping Plover broods were observed for a total of 26.2 h. A chick was seen to pass near a crab only once, and in that instance, there was no response from the crab.

After leaving the nest and exclosure, chicks were almost always found foraging in vegetated areas, principally on the low foredunes ($n = 18$). Chicks from Nest Five were found on high dunes because low foredunes were uncommon in their territory. This brood was seen once on the foreshore of Wild Beach on the day after it left the exclosure. Surviving chicks from all broods were taking 5–10 m forays away from the attending parent by 1.5 days, often in divergent directions. The attending adult was often seen following after a rapidly moving chick. Typically the attending adult stayed near the chicks, outside the vegetation, while the other adult stationed itself near the berm, standing sentinel and frequently feeding on the foreshore. During midday chicks alternated between foraging and resting in the shade of vegetation. The parent typically moved the chicks back to the same general area each evening to brood. Typical brooding areas were in shell hash (broken shell fragments) on the backshore near foredunes, a few meters from dune vegetation.

Activity periods of birds and crabs showed little overlap once the chicks left the nest. Parent birds began brooding chicks as each evening became cool, from about 18:30 to shortly before 20:00 (19:05 ± 28 min, $n = 8$), until chicks ceased making forays altogether, typically between 19:00 and 20:30 (20:00 ± 38 min, $n = 8$). First sightings of crabs moving to the foreshore occurred about the same time that chick activity fully ceased (19:51 ± 9 min, $n = 7$ nights). Crab activity increased

during the following hour, and chicks were brooded during the peak of activity. In the morning, crabs migrated from the foreshore to their burrows before dawn (04:16 ± 11.3 min, $n = 2$ mornings), and before broods were seen to become active. Some crab activity persisted throughout the day, generally restricted to the vicinity of burrows whose densities increased from the dunes toward the berm.

No instances of crab predation on bobwhite chicks occurred, although more than 30 encounters were observed in 12 hours of diurnal and nocturnal observation. In the one case in which a crab seized a quail chick that was precipitously deposited next to its burrow, the crab promptly released the chick unharmed and retreated to its burrow. Most commonly, crabs showed no response to chicks that wandered nearby within visual range. Crabs were attracted to, and fed readily on, cracked oyster and chicken during the same intervals in which chicks were presented, demonstrating the crabs' willingness to forage and feed. However, crabs routinely ignored dead quail chicks, even when they physically contacted them in the course of foraging.

Crab interactions with adult Piping Plovers.—Interactions between incubating adult Piping Plovers and approaching crabs were variable. Plovers either remained on the nest ($n = 4$) or flushed ($n = 4$). Flushing typically occurred while the crabs were further than 0.5 m from the nest cup ($n = 3$), but once not until the crab approached within 10 cm. Defensive encounters initiated by the plovers could involve both parents ($n = 2$). In the four instances in which birds responded to crabs, the minimum length of engagement in the video field was 2 min (120 ± 49 s, $n = 4$). However, adults left the nest cup unattended for about 5 min (307 ± 197 s, $n = 4$), presumably continuing the defense out of the camera's view.

Aggressive displays by incubating adult plovers against approaching crabs were largely ineffectual. Crabs generally remained motionless or maintained course ($n = 3$) when confronted by adult plovers advancing slowly with uplifted wings, but sometimes they ran when charged by a displaying bird ($n = 2$). In one instance, a crab whose course would have bypassed the nest was deflected onto the nest while veering from the displaying parent.

Thirteen encounters between crabs and adult plovers with unfledged chicks were observed, with variable behavior by the plovers. Once, an adult passed within 10 cm of a crab with no apparent response. Where interactions occurred ($n = 12$), plovers always initiated them, although the crab was 8–50 m from the brood. Plovers would approach and display within 10–20 cm of the crab. Birds were seen feigning and leading crabs toward the foreshore (max distance = 10 m, max time = 4 min, $n = 3$). Three encounters involved both parents.

Adult plovers appear to associate the presence of burrows with ghost crabs. A burrow that was near a nest was ignored for the first 85 hours of video observation, but was closely inspected by the adult plovers on 11 separate occasions in the final 11 hours of observation after a crab had approached the nest from that direction. Burrows were also investigated on the beach by parents with hatched broods ($n = 2$).

Plover behavior and mortality.—Although we observed no instances of Piping Plover mortality directly attributable to predation by ghost crabs, we documented other factors that might directly or indirectly contribute to the low fledging success on Wild Beach. Hatching asynchrony (substantial time, e.g., >24 hrs between hatching of the first and final eggs in a given clutch) was responsible for the only mortality for which a cause could be established, and the only mortality to occur prior to hatching. Hatching asynchrony showed a strong seasonal correlation in this study. Six clutches of eggs were laid on Wild Beach in 1994 (Table 1). For the two monitored broods in June, hatching was highly synchronous. The time between the hatching of the first egg and the last egg in an entire clutch averaged 104 min. In the three July broods, duration of hatching averaged at least 1680 min. The asynchrony contributed directly to the abandonment of an egg, which was determined to be viable (Refuge Staff pers. comm.).

Of 23 chicks that hatched on Wild Beach in 1994, two fledged. Half the mortality occurred in the first two days, and 75% by day five (Fig. 1). This pattern of chick loss soon after hatching is typical for the species, but even more pronounced than reported in previous studies (most mortality in the first 10

TABLE 1. Data for broods of Piping Plover (*Charadrius melodus*) hatching on Wild Beach, Assateague Island, 1994. Based on six clutches laid on Wild Beach; nests 2, 3, 5 and 6 were monitored via video camera.

	Nest 1	Nest 2	Nest 3	Nest 4	Nest 5	Nest 6
Hatch date	June 10	June 10	June 16	July 4–6	July 6/7	July 8/9
Hatch duration	?	20 min	3 hr 08 min	>36 hr	>24 hr	>24 hr
Interval to walk	?	1 hr	1–2.5 hr	?	6 hr	5 hr
Time nest abandoned	?	18:49	16:10	?	16:37	15:44–18:45
Survival, days (time of death where known[a])						
chick A	0.5 (n)	0.5 (n)	1.5	?	1–2 (d)	0.5 (n)
chick B	0.5 (n)	0.5 (n)	1.5	?	3–4 (d)	0.5–1.5 (n)
chick C	7	1 (d)	fledged	9	4 (d)	1–2
chick D	16	1.5	fledged	13	never hatched	4–5

[a] Where frequency of observation permits, the time of disappearance of chicks is given as day (d) or night (n).

days; MacIvor 1990; Patterson 1988; U.S. Fish and Wildlife Service 1993). Mortality of chicks in all the June broods was highly concentrated in the first 48 hours (67%), with 25% occurring during the first night. In the monitored July broods, mortality did not occur during the first night, but was spread rather uniformly over the first week.

We could not document the cause of mortality and the fate of "disappeared" chicks. All mortality on Wild Beach occurred after broods had left the nest. Where confirmed sightings allowed the time of disappearance of chicks to be established with some certainty, chicks were as apt to vanish during the night as during the day (Table 1). Five chicks disappeared between sunset and 09:00, and five between 08:00 and 19:00. Signs of direct predation were never found.

Differences in diel activity patterns between June and July broods were documented through video observation, and indicated differences in potential for prey acquisition and for practicing locomotor and feeding behaviors during the first day of life. Hatching was highly synchronous in June, but asynchronous in July (Table 1). Chicks emerged from the nest cup for brief excursions as soon as 1 hour after hatching in the June broods, but after 5–6 hours in the July broods (Table 1). For June broods (2 and 3), chicks spent extended periods in the shade of vegetation near the nest, or out of the camera's field of view, before returning to the brooding parent, and were active throughout the day. July chicks spent little time away from the nest and were continually brooded during the hot midday.

Newly hatched chicks in all broods left the exclosure between 16:00 and 19:00 (Table 1). The chicks ranged from 4 to 12.5 hours in age, and exhibited obvious age-related differences in coordination for walking and running, both within and between broods.

Once the nest was abandoned, it was no longer possible to observe broods by using video. However, in one of the asynchronous broods, detailed observation of brooding and foraging of day-old chicks was made by video on three chicks that spent their first day post-hatch (July 7) in the area of the nest while the fourth egg was still being incubated. There was an initial peak in activity of the chicks (50% of each hour spent moving about) between 05:00 and 07:00 and another (30%) after 14:00. Activity remained below 10% between 09:00–13:00, and fell to zero at 12:00 when chicks were continuously brooded. Foraging, as seconds per hour that a chick spent
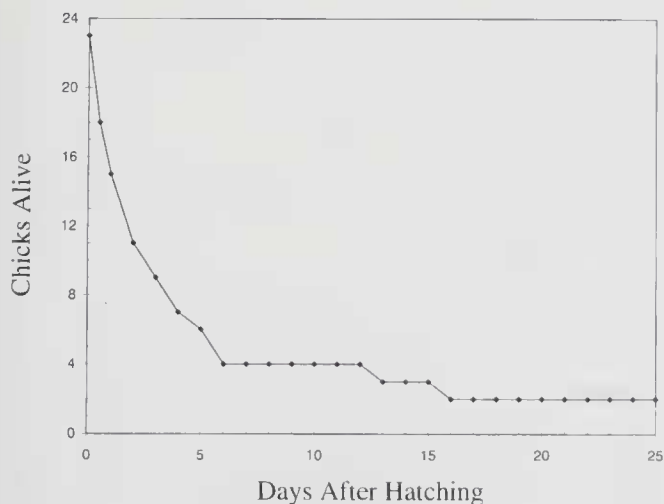

FIG. 1. Chick survival, broods 2–6.

in hunt and peck behaviors, was congruent with the activity pattern (300 s/hr 05:00–07:00, <10 s/hr 11:00–12:00).

DISCUSSION

Crab predation on Piping Plover chicks.— Ghost crabs do not appear to be directly responsible for the poor breeding success of Piping Plovers on Wild Beach on Assateague Island. Ghost crabs showed no predatory response to nearby chicks of Piping Plover or Northern Bobwhite, and occasionally even ran away from chicks. Since crabs that were active during daylight hours readily fed on other prey, we conclude that chicks (at least Northern Bobwhite) are not preferred prey.

Beyond the crabs' apparent lack of interest in chicks, there is temporal and spatial separation in crab and chick activity that further reduces, but does not eliminate the likelihood of interactions. Ghost crabs are principally nocturnal; they become active after sunset and migrate to the foreshore to prey on macroinvertebrates. Crabs leave the foreshore and return to burrows by dawn. During the early morning hours, they may be active near their burrows, spending time on burrow repair, defense, and intraspecific aggression, until they are confined below the surface by microclimatic conditions. Crab activity is extended on days with low desiccation risk (pers. obs.). Although breeding adult plovers may forage extensively on the foreshore at night (Staine and Burger 1994), unfledged chicks on Wild Beach are almost entirely diurnal. During the periods when crabs are most active, chicks are being continuously brooded, at least through the first week post-hatching when most chick mortality occurs. In addition to temporal separation, spatial separation of chicks and crabs was also evident. Only once was a brood seen foraging in the intertidal prior to two weeks post-hatching; all other foraging occurred within 5 m of the dunes onto the backshore, and hence was well inland of the berm and the densest aggregation of crab burrows.

The possibility of occasional predation on foraging chicks by crabs cannot be dismissed. Only a single documented event (Loegering et al. 1995) has occurred in over 116 h of direct observation in this and other studies (Patterson 1988, 44 h; Loegering 1992, 46 h; this study, 26 h). Based on our observations, predation is most apt to occur when a chick startles a crab, especially one that has been recently defending its burrow. Aggression between crabs peaks during the early morning hours as they compete for burrows. Land crabs of several species will jump, either on potential prey, or as part of aggressive encounters (Herreid 1963, Evans et al. 1976, pers. obs.) On video we observed an hours-old plover chick careening head first into a crab burrow. Had the burrow been occupied, the chick might have been killed. Nevertheless, our data indicate that stalking and killing of chicks by crabs is highly unlikely.

Crab predation on eggs.—Video observations in our study show that ghost crabs that make contact with Piping Plover eggs investigate the eggs as potential prey items, using stereotypical tasting behaviors. Crabs showed the same behavior toward surrogate eggs of *Coturnix japonica* and *Colinus virginianus* on the beach and in the lab. However, the claws of the largest crabs on Wild Beach do not have a gape large enough to directly crush a plover egg, and no predation was observed.

Nevertheless, ghost crabs are confirmed, though infrequent, predators of Piping Plover eggs on barrier islands in Virginia (Watts and Bradshaw 1995; Refuge staff, this study) and North Carolina (S. Philhower, pers. comm.). Viable eggs have been found in crab burrows (S. Philhower, pers. comm.), but from known crab behavior and observations during this study, we conclude that ghost crabs are most likely to attack or manipulate eggs that are rotting, cracked, or dirty. Crabs use dactyls and claws for contact chemoreception, and distance olfaction to track odor plumes to the source of a smell (Wellins et al. 1989). Ghost crabs that encounter a large food parcel (e.g., a dead fish) typically dig a burrow immediately adjacent to it, which provides security for extended scavenging. Crabs that burrow next to a nest may do so because they identify plover eggs as potential food. For instance, a ghost crab burrow was found immediately adjacent to a Piping Plover nest on a beach 10 km south of Wild Beach when refuge staff inspected the nest after it was abandoned by the adults after 35 days of continuous incubation (normal development time is 27 d). The eggs were missing. Excavation of the crab burrow yielded three of the four eggs, one of

which was emitting a powerful smell. The missing egg was assumed to have been consumed by the crab. A crab that has experienced eggs as prey may subsequently recognize intact and odor-free eggs as food through non-associative learning (Evans et al. 1976). It is unclear whether broken eggs that have been found in crab burrows were already cracked, and hence emitting an attractive odor, or were cracked from hitting each other in the burrow. Whether instances of nest predation by ghost crabs were initiated as scavenging or as predation, the end result is that some viable eggs are lost to crabs. Nevertheless, we conclude that egg predation by ghost crabs cannot account for poor breeding success of Piping Plovers on Wild Beach.

Piping Plover response to crabs.—Whatever the actual threat from ghost crabs, adult Piping Plovers treat them as potential predators. We observed 16 instances in which one or both adults engaged in extensive displays against crabs, and in 5 cases, the defense left hatched broods unguarded. Further underscoring the perceived threat from crabs, adult plovers seem able to connect the presence of burrows with ghost crabs, and invest time and energy in investigating burrows.

The presence of abundant ghost crabs may create indirect problems for plovers by several mechanisms related to the adults' perception of crabs as potential predators. First, obvious responses to ghost crabs may alert truly dangerous predators, both avian and mammalian, to the location of the brood at the very time the parents are busy elsewhere and leave it undefended. Second, more frequent alarm and defense behaviors carry an energetic cost (reviewed in Walters 1984). Finally, it is possible that the abundance of crabs on the backshore induces the adult Piping Plovers to shepherd their broods away from the foreshore, where forage might be more abundant and have a higher water content. Broods elsewhere on Assateague Island are routinely taken to the foreshore (refuge staff, pers. comm.).

Given the minimal direct threat posed by ghost crabs, and the potential negative consequences of frequent display and restricted foraging, it seems maladaptive on the part of the adult Piping Plovers to treat crabs as dangerous predators. Natural selection acting on adult defensive behavior should have eliminated the behavior if ghost crabs are not significant predators and if engaging in defense towards ghost crabs increases the likelihood of predation by other predators. However, lack of sufficient genetic isolation between birds breeding in areas with and without ghost crabs would preclude such selection. Instead, some Charadriidae appear to recognize several animal categories, including avian, mammalian (with a subset of ungulate), reptilian and "other". They have evolved unique displays to each group (reviewed in Gochfield 1984). They generally distinguish potential predators from non-predators, especially among birds, thereby minimizing false alarms (Walters 1990). However, they seem less discriminating about other intruders, lumping disparate taxonomic groups into a category of "potential threat" in an "urgency of response scheme" (Walters 1990). Perhaps Piping Plovers indiscriminately categorize anything terrestrial but "neither a large mammal nor a snake", and moving near a nest or near chicks, as requiring immediate alarm. This group might include dangerous predators such as rats or mustelids to which immediate alarm would be adaptive. If one postulates that organisms such as crabs and turtles, which do not pose a significant threat but which do elicit alarm responses from parenting plovers (refuge staff, pers. obs.), are lumped into the same "dangerous predator" category in the alarm response hierarchy, the apparently maladaptive alarming by Piping Plover parents could be explained. Given the large geographic range and variety in breeding habitat, with concomitant and unpredictable variation in the suite of predators, mounting a defensive display against anything novel in the area of the brood might have at least neutral if not beneficial effects on fitness.

Correlations between low fledging success and high ghost crab abundance.—We hypothesize that high ghost crab abundance and low fledging success of Piping Plovers have a correlative, not causative, relationship. Three factors contribute to the correlation: beach and dune morphology, climate, and parental behavior.

Ghost crabs are most abundant on high energy beaches backed by high dunes. The high dunes provide overwintering habitat in which crabs are able to burrow below their lethal iso-

therm (6–8° C) before being blocked by the water table (T.G.W., unpubl. data), while high-energy beaches provide habitat for the crabs' preferred prey (Wolcott 1978). However, beaches that are backed by dunes and that lack low-lying moist habitat away from the surf, may be poorer habitat for raising Piping Plover broods, even in the absence of crabs. On Assateague Island, slower growth with concomitant reduced survival has been documented for chicks reared on an ocean beach, compared with chicks from other areas with low-lying moist habitat for foraging (Loegering and Fraser 1995). Prey abundance (measured in the wrack zone) and foraging rates were lower on the ocean beach as well. Wild Beach lacks the low-lying moist areas that are the major foraging habitat for young plover broods in the more productive breeding areas on Assateague. Even the steep intertidal with its sharp escarpments may pose a physical barrier to young broods moving to the foreshore.

During the same time as our study, over 90% of chicks successfully fledged on a site approximately 400 m inland from our site, with extensive moist low-lying forage but no access to the beach. Similarly 91% fledging success occurred on a low energy beach at the southern tip of Assateague Island, with extensive backshore foraging areas. Meanwhile less than 10% of chicks fledged on Wild Beach, a percentage similar to its long-term average (1988–1994, U.S. Fish and Wildlife 1994). Poor forage is more likely to contribute to the unusually high chick mortality on Wild Beach than direct ghost crab predation.

Climate and latitude probably play a role in the plover-crab relationship. From their northern limit in New Jersey through the southern limit of plover breeding in North Carolina, ghost crabs increase in size and abundance (U.S. Fish and Wildlife Service 1996). Presumably, at lower latitudes more adult crabs are able to successfully overwinter, emerge earlier in the spring, have a longer active season, and grow to a larger adult size. Higher abundance of large crabs leads to more encounters between birds and crabs, with an increase in adverse indirect effects on Piping Plovers.

The hotter summer temperatures associated with lower latitudes may directly affect brood survival of Piping Plovers. High daytime temperatures may speed the rate of embryo development and lead to greater hatching asynchrony (reviewed in Magrath 1990, Shields 1998). Asynchrony may contribute to mortality directly by causing abandonment of viable, late eggs, and indirectly, by reducing the cooperative attendance by adults of the hatched young. In our study, severe asynchrony also resulted in broods having chicks of very different locomotor capabilities, which could increase the likelihood that chicks will become separated from one another and lost.

Desiccation poses an even more immediate danger to the chicks. Piping Plovers acquire water from their food and thermoregulate by panting (Haig 1992). During the critical first day, broods hatching in hot weather during our study showed a reduction in foraging time and activity compared to broods hatching in cooler weather. Should heat cause a persistent shift in activity, it implies that during hot weather intake of food and its included water is lowered at the same time that evaporative losses become greater. Understanding the relationship between elevated temperatures, asynchrony, and brood survival is critical to informed management decisions at the southern end of the Piping Plover's breeding range.

The behavior of the adult plovers to the perceived threat of the crabs compounds the problem of desiccation because the adults apparently restrict their broods to the duneline, where forage is sparser and drier. On longer time scales, restricted feeding times and poor forage will result in slow growth and increased mortality (Loegering and Fraser 1995). The threat perceived by adult plovers of ghost crabs on the Wild Beach may act as a barrier between broods and the richer food resources of the foreshore.

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